

Visual transients reveal the veridical position of a moving object

Article (Published Version)

Kanai, Ryota and Verstraten, Frans A J (2006) Visual transients reveal the veridical position of a moving object. *Perception*, 35 (4). pp. 453-460. ISSN 0301-0066

This version is available from Sussex Research Online: <http://sro.sussex.ac.uk/id/eprint/43994/>

This document is made available in accordance with publisher policies and may differ from the published version or from the version of record. If you wish to cite this item you are advised to consult the publisher's version. Please see the URL above for details on accessing the published version.

Copyright and reuse:

Sussex Research Online is a digital repository of the research output of the University.

Copyright and all moral rights to the version of the paper presented here belong to the individual author(s) and/or other copyright owners. To the extent reasonable and practicable, the material made available in SRO has been checked for eligibility before being made available.

Copies of full text items generally can be reproduced, displayed or performed and given to third parties in any format or medium for personal research or study, educational, or not-for-profit purposes without prior permission or charge, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way.

Visual transients reveal the veridical position of a moving object

Ryota Kanai[¶], Frans A J Verstraten

Psychonomics Division, Helmholtz Research Institute, Utrecht University, Heidelberglaan 2, NL 3584 CS Utrecht, The Netherlands; e-mail: r.kanai@fss.uu.nl

Received 15 March 2005, in revised form 2 July 2005; published online 8 February 2006

Abstract. The position of a moving object is often mislocalised in the direction of movement. At the input stage of visual processing, the position of a moving object should still be represented veridically, whereas it should become closer to the mislocalised position at a later processing stage responsible for positional judgment. Here, we show that visual transients expose the veridical position of a moving object represented in early visual areas. For example, when a ring is flashed on a moving bar, the part of the bar within the ring is perceived at the veridical position, whereas the part outside the ring is perceived to be ahead of the ring as in the flash-lag effect. Our observations suggest that a filling-in process is triggered at the edges of the flash. This indicates that, in early cortical areas, moving objects are still represented at their veridical positions, and the perceived location is determined by the higher visual areas.

1 Introduction

The position of a moving object is perceptually mislocalised towards the direction of movement in various situations (Ramachandran and Anstis 1990; De Valois and De Valois 1991; Sheth and Shimojo 2003; Whitney et al 2003; Kanai et al 2004). For example, when a flash physically coincides with a continuously moving object, the position of the moving object is perceived to be ahead of the flash. This visual phenomenon is called the flash-lag effect—FLE (Hazelhoff and Wiersma 1924; Metzger 1932, in Mateeff and Hohnsbein 1988; MacKay 1961; Nijhawan 1994).

At the input level of vision (eg the retina), a moving object and a flash should be aligned as they physically are.⁽¹⁾ Even after the retina, the positional representations in the very early stages should remain veridical. Only after certain stages of visual processing does the neural representation correspond to the perceived and sometimes illusory position, as opposed to physical position. In this hierarchical view of visual processing, there is a transition from a veridical representation to a more perceptual representation as the processing proceeds to a higher stage. Usually, stationary objects are perceived roughly at the veridical location. Therefore, we cannot experimentally dissociate the neural responses from the physical input and the neural representations corresponding to the perceived location. In mislocalisation illusions, however, the perceived position can be dissociated from the physical position on the retina. Thus, mislocalisation illusions such as the FLE offer an opportunity for isolating the neural substrates representing our sense of space in the visual brain.

In the present study, we report a new visual phenomenon that illuminates the issue of physical versus perceived (or illusory) position. In the classical FLE stimulus, as shown

[¶]Present address: Division of Biology, California Institute of Technology, M/C 114-96, Pasadena, CA 91125, USA.

⁽¹⁾ Motion-sensitive neurons in the retinal ganglion cells of rabbit and salamander respond earlier to a moving stimulus (Berry et al 1999). However, whether a similar direction-dependent excitation mechanism, which would contribute to the FLE, exists in the primate is unknown. Given our present knowledge of the primate retina, we cannot completely exclude the possibility that in humans the FLE begins as early as in the retina.

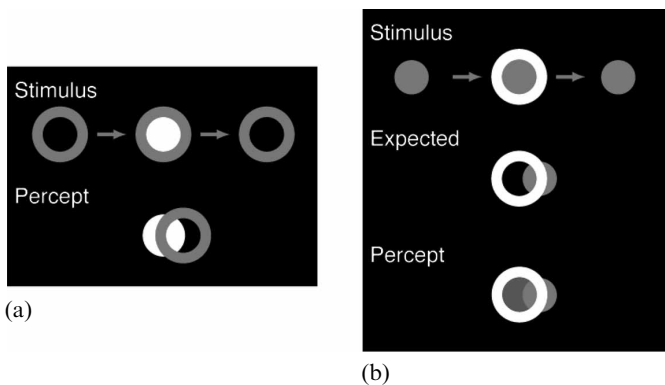


Figure 1. Flash-lag effect (FLE) (a) versus real position recovery (b). (a) A typical FLE stimulus is shown at the top. Here, a red disk (shown gray) moves from left to right. Midway, the inside of the disk is flashed. In the percept, the moving ring is perceived at a position shifted in the motion direction, whereas the flash remains at the veridical position. In this stimulus, the flash and the ring are dissociated, and a crescent black region is perceived within the ring (bottom). (b) A typical stimulus for the recovery effect (top). Here, a red disk moves from left to right. Midway, a white ring physically enclosing the moving disk is flashed. The FLE predicts the percept when the ring and the flash are dissociated (middle). However, one perceives not only the moving disk at a position shifted in the motion direction, but also the region within the flashed ring is completely filled with the colour of the moving disk (bottom).

in figure 1a, the inside of a moving ring is flashed. There, the flash lags behind the moving ring and there is a crescent shaped ‘perceived void’, that is a hollow region within the ring filled with the same colour as the background (eg Eagleman and Sejnowski 2000; Khurana et al 2000; Nijhawan 2001). In our illusion, the ordering of the ring and the disk is reversed, ie we flash a ring surrounding a moving disk (figure 1b). Although this configuration does not seem fundamentally different from the classical FLE, an interesting percept, which is not expected from the classical FLE study, arises: the moving disk is perceived not only ahead of the flashed ring, as the FLE predicts, but also within the ring—the veridical position of the moving disk. In other words, the disk is perceived at two locations simultaneously, one at an extrapolated position and the other at the real position. This perceptual effect demonstrates that the veridical position—which is usually not perceived—is made consciously visible by the flash.

1.1 Initial observations

We created a series of related stimuli to capture the basic characteristics of the effect. First, we used a smaller moving disk so that it does not completely fill the hollow area of the flashed ring (figure 2a). In other words, the edge of the moving disk is not attached to the inner edge of the flashed ring. In this case, the recovery of the veridical position was not observed, and just the standard FLE was observed. Second, we used a moving ring (instead of a disk) fitted within the flashed ring (figure 2b). The inside of the moving ring was empty (ie filled with the background colour). Nevertheless, the inside of the flashed ring was perceptually filled with the red, including the empty hole of the moving ring. Third, a ring was flashed on the central part of a long, moving vertical bar (figure 2c). The part of the bar falling within the ring was perceived at the veridical position with respect to the flash, lagging behind the rest of the bar outside the frame.

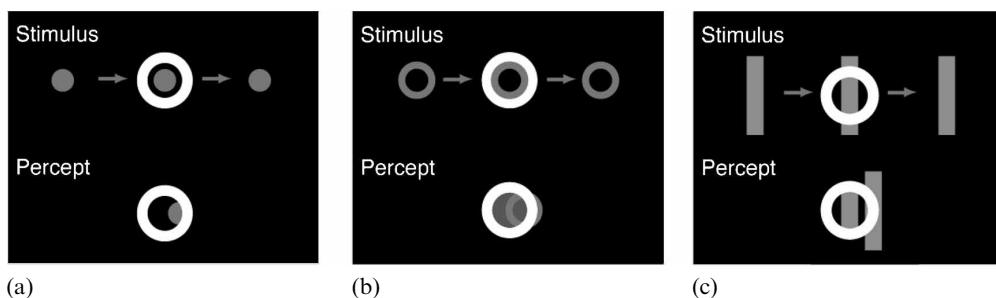


Figure 2. Variations of the recovery of the veridical position. (a) When the moving disk is not attached to the inner edge of the flashed ring, the real position is not recovered. (b) In the case where the moving disk has a hollow region within itself, real position recovery is observed and the hole of the moving disk is filled. (c) When a ring is flashed on a moving bar, the part of the bar within the ring is recovered.

2 Experiment 1

The initial observations suggest the involvement of a filling-in process in the recovery of the veridical position. One important characteristic of filling-in is that the propagation of colour towards the inside of flashed edges takes time (Paradiso and Nakayama 1991). For instance, the inside of a flashed square is often perceived as less vivid than the area near the edges, or sometimes not filled-in at all (Macknik et al 2000). If the filling-in is involved in the recovery effect, the vividness of the recovered veridical position should inversely scale with the distance between flashed edges. In experiment 1, we directly address this issue by systematically measuring the effect of distance on the vividness of the recovered part of a moving stimulus.

In order to obtain a clear percept of the recovery effect, the stimulus needs to satisfy several conditions. First, the speed of the moving object needs to be sufficiently fast so that its illusory position created by the FLE is spaced well apart from the veridical position. This is necessary for observers to allow them to identify clearly the spatial offset. Also, motion needs to be sufficiently smooth and continuous. With discrete motion stimuli (ie apparent motion), each frame persists longer in the percept, resulting in a percept of multiple objects even without a flash. Also, we wished to make the stimulus as symmetric as possible with respect to the fixation so that we could minimise contamination of the effects by eye movements. Under these constraints, we chose an expanding ring as a moving stimulus, as it is symmetric in all directions.

2.1 Methods

2.1.1 Observers and apparatus. Six observers participated in this experiment including one of the authors (RK). All observers had normal or corrected-to-normal vision. The stimuli were controlled by an Apple Macintosh running Matlab and presented on a 22-inch CRT monitor with a resolution of 1280×1024 pixels at 75 Hz refresh rate. The viewing distance was 57 cm and head movements were restrained by a chin-rest.

2.1.2 Stimuli and procedure. The stimulus was an expanding black ring (speed, 15 deg s^{-1} ; line thickness, 0.4 deg) against a gray background (46 cd m^{-2}). When the ring reached the eccentricity of 5.6 deg , a flash consisting of dots arranged in a circle was presented for one frame (13 ms) on the ring (see figure 3b). The diameter of the dots was 0.4 deg and their luminance was 92 cd m^{-2} . The flash was made with a variable number of equally distributed dots (4, 6, 8, 10, 12, 24, and 32).

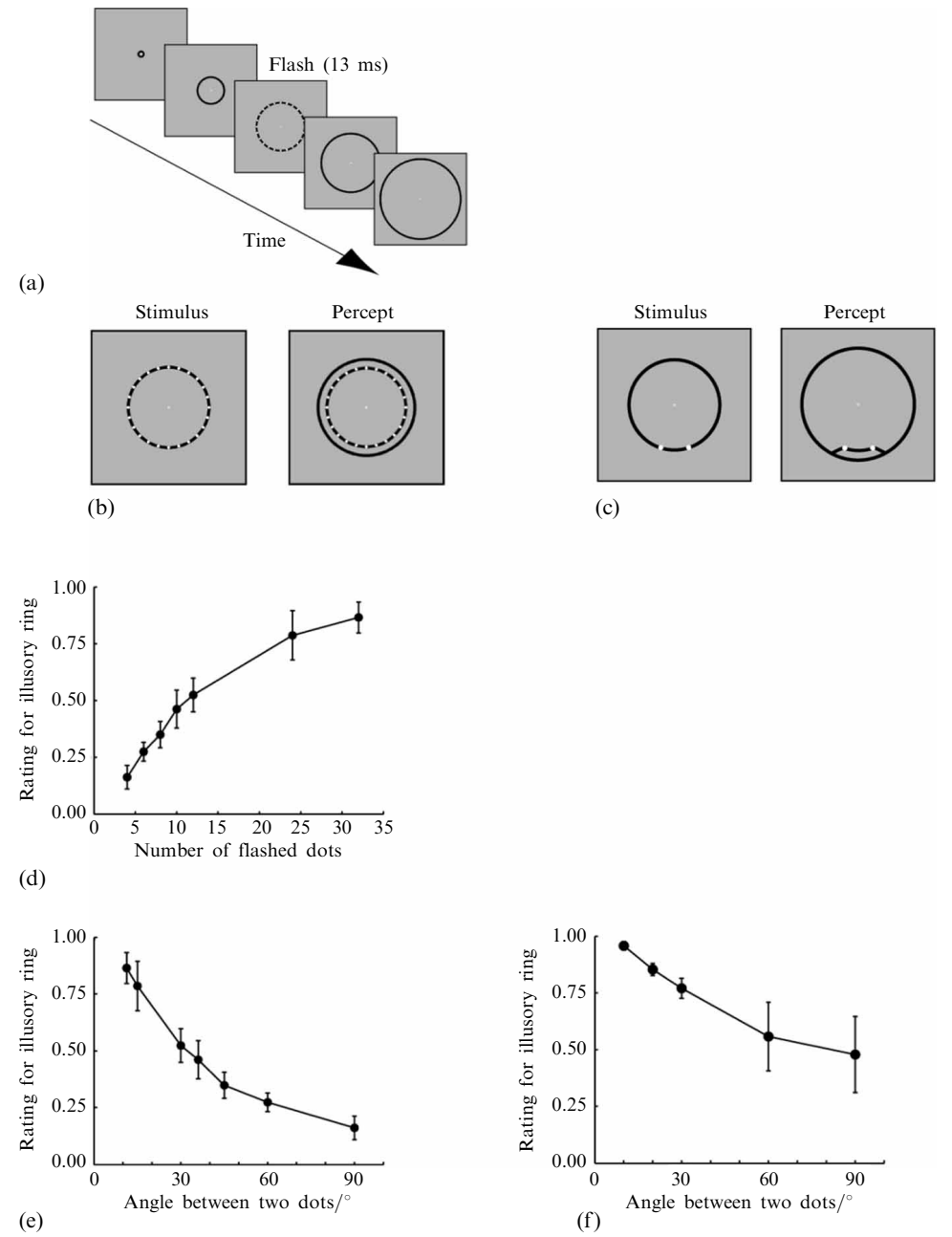


Figure 3. Illustration of stimuli and the results. (a) The stimulus is an expanding ring. (b) White dots are flashed on the black ring as shown in the left panel. This results in the percept with two rings as shown in the right panel. (c) The stimulus and a typical percept in the two-dot experiment are illustrated. (d) The vividness of the recovered ring as a function of the number of flashed dots (six subjects). Error bars indicate ± 1 SEM. (e) The same data re-plotted as a function of the separation angle between two dots. (f) The results of two-dot experiment: instead of many dots, only two dots were used and their separation angle was varied. The vividness of the arc enclosed by the two dots is plotted as a function of the separation (six subjects). Error bars indicate ± 1 SEM.

The observers performed a rating task where they were required to report the vividness of the black ring between the flashed dots. They rated the vividness from the following choices:

- (i) no ring was perceived;
- (ii) a faint ring was perceived, but was not as vivid as the moving one;
- (iii) a ring as vivid as the moving one was perceived.

For each condition 20 samples were made. Thus each observer had a total of 140 trials (7 different numbers of dots \times 20 samples). The observers' ratings were scaled between 0 and 1 by giving a score 0 to choice 1, 0.5 to choice 2, and 1 to choice 3. High score indicates a more vivid percept of the veridical position.

As an auxiliary experiment, we repeated the same experiment with just two dots, while varying the spacing between them (10° , 20° , 30° , 60° , or 90°). The two dots were presented in the lower visual field and were symmetrical with respect to the midline (figure 3c). When the recovery is effective (ie at small separations), the recovered part of the ring is typically perceived as connected to the rest of the ring as illustrated in figure 3c. However, the percept of the lines connecting the recovered arc to the rest of the ring is usually very faint. Therefore, observers were asked to base their judgments only on the vividness of the arc between the two flashed dots. The same six observers participated.

2.2 Results

The results are shown in figure 3d. Our initial motivation in this experiment was to test whether the vividness of the recovered ring depends on the distance between the flashed dots. If the recovery is indeed mediated by a filling-in mechanism, the vividness should increase by reducing the separation between the flashed dots.

The vividness of the ring at the veridical position increased as more dots were flashed (Spearman rank-order correlation, $R_s = 0.8116$, $p < 0.001$). This is consistent with the hypothesis that a filling-in process is involved in the recovery effect, because the percept of the recovered ring was more vivid at small separations between the flashed dots (figure 3e). This means that the recovery is not triggered by some transient stimuli, but spatial proximity is crucial for it. In other words, the recovery involves a local interaction.

However, the recovery could also depend on the total number of dots in a flash; with a larger number of flashed dots, the total magnitude of flash becomes larger, resulting in a stronger effect. We therefore repeated the same experiment with just two dots, while varying the distance between them (10° , 20° , 30° , 60° , or 90°). The two dots were presented in the lower visual field, symmetrically with respect to the midline. Observers made judgments on the vividness of the arc made by the two dots.

The results from the same six observers are shown in figure 3f. It can be seen that when the separation was small, the percept of the black ring at its veridical position was more vivid (Spearman rank-order correlation, $R_s = -0.7039$, $p < 0.01$). Thus the distance between the dots enclosing the recovered region determines the vividness of the recovered veridical position. As mentioned earlier, the dependence of the vividness on the separation between the flashed dots is consistent with the prediction based on the involvement of filling-in.

3 Experiment 2

We further examined the temporal characteristics of the effect; these help us to understand how a flash interacts with a moving object. For example, if the flash interacts with the residual activity of the moving object, which by itself is no longer strong enough to give rise to a conscious percept, the flash presented even after the moving object should produce a similar, if less vivid, recovery effect. On the other hand, if the

flash interacts only directly with the concurrently present signals stemming from the moving stimulus, the maximum recovery effect should be obtained with synchronous presentation of the flash.

To address these temporal issues, we used the stimulus with 24 dots, but the dots were flashed at a variable timing (SOA), both before and after the moving ring had passed the eccentricity of the flashed dots (5.6 deg).

3.1 Methods

3.1.1 Observers and apparatus. The same six observers participated. The apparatus was the same as experiment 1.

3.1.2 Stimuli and procedure. The stimulus was the same expanding black ring (speed: 15 deg s^{-1} ; thickness, 0.4 deg) against a gray background. 24 white dots were flashed (13 ms) at the eccentricity of 5.6 deg with a variable timing with respect to the time when the expanding ring arrived at the same eccentricity. The relative timing, or stimulus onset asynchrony (SOA) between the flash and the ring at the eccentricity, was varied between the values of -120 , -80 , -53 , -26 , 0 , $+26$, $+53$, $+80$, and $+120$ ms. Negative SOAs indicate that the flash was presented before the ring reached the given position, whereas positive SOAs indicate that the flash was presented after the ring passed that position.

The observers again made a subjective rating as described in section 2. Each observer performed 20 trials per condition, resulting in a total of 180 trials (9 conditions \times 20 trials). The order of the conditions was randomised across trials.

3.2 Results

The results are shown in figure 4. The effect of SOA on the vividness rating was significant (repeated-measures ANOVA: $F_{8,40} = 14.52$, $p < 0.001$). The percept of the recovered veridical position was strongest when the flash physically coincided with the moving stimulus. Flashing the dots after the ring had passed did not lead to the recovery of the veridical position of the ring. On the other hand, flashing the dots before the arrival of the ring produced a weak effect. This is difficult to interpret, because around that time (in negative SOAs), the illusory position of the ring could overlap the position of the flashes. Another possible cause for the report of the vivid ring for the negative SOA condition is the longer persistence of the flashed dots than that of the moving ring (eg Burr 1980). In other words, flashed dots presented before the ring reaches the position of the flash stay visible until the expanding ring reaches that point. This could also result in the report of a veridical ring under the flashed dots. Notwithstanding this, the data certainly support the main point that a vivid percept of the veridical position is attained with the flash that physically overlaps the moving stimulus in space and time. This indicates that the flash interacts directly with

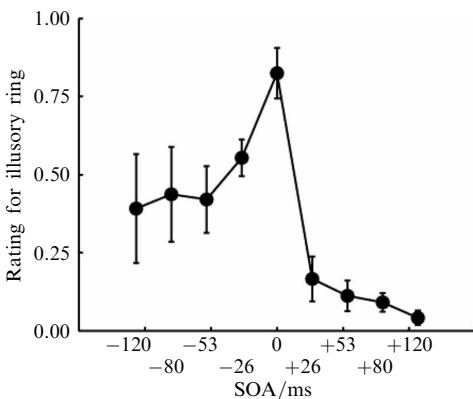


Figure 4. The results of the timing experiment. The vividness of the ring is shown as a function of temporal separation between the flash frame and the frame containing the ring at the same location as the flash (six subjects). Positive SOAs indicate that the flash was presented after the expanding ring has passed, whereas negative SOAs indicate that the flash was presented before the ring has arrived at the eccentricity. Note that maximum vividness was attained when the timing was synchronous (SOA = 0). Error bars indicate ± 1 SEM.

the signals from the moving stimulus and that, at the time this interaction occurs, both the flash and the moving stimulus are represented at their veridical positions at the correct timing.

4 Discussion

We have shown that the veridical position of a moving object can be made visible by presenting an adjoining stimulus transiently. The effect is specific to the region enclosed by the transient. The percept is most vivid when the flash physically coincides with the moving stimulus in space and time. These findings indicate that the interaction occurs at the early processing stage where the moving stimulus is still represented at the veridical position.

Our observations suggest that a filling-in process is involved in the recovery of the veridical position. This is further supported by our experiments showing that the recovery is limited to the region enclosed by flashed stimuli (the two-dot experiment; figure 3e). Filling-in is usually based on edge information in that the feature information of colour or brightness propagates from the edges and fills-in the enclosed area (Paradiso and Nakayama 1991). When the moving disk was not directly bordering the flashed ring, the recovery was not observed (figure 2a), indicating the need for edge information. That is, the recovery is not as general as recovering any picture within a flashed ring. Further, our observation as shown in figure 2b indicates that the recovery is mediated by the edge connected to the flash, because the edge information (white–red) is sufficient to fill-in the entire region within the ring including the empty spot. Finally, the effect is specific to the enclosed area, but not outside the ring (figure 2c), again consistent with our filling-in interpretation.

We have shown that the opening between two flashes creating the edges needs to be small in order to create a vivid percept of the veridical position. This is again consistent with the filling-in interpretation. For example, if a colour-filled stimulus is presented very briefly, the inside of the stimulus is often not perceptually filled. This is because the filling-in process cannot be completed within a short duration of time (see Macknik et al 2000). With increasing distance between edges, longer time is required for the filling-in to be completed and the vividness fades.

Generally, the filling-in process is mediated within the early visual areas where the visual field is retinotopically organised. The percept of veridical position implies that the positional representation of a moving object is still maintained at the veridical location in the areas responsible for filling-in. Therefore, subjective judgment on the position of a moving object should be based on the information encoded at later stages. Put differently, the veridical representations in these areas are not directly reflected in our subjective perception. They are made visible only when incited by transient stimuli.

In this study, we have demonstrated that the flash captures the implicit sensory signals from the moving object, which is unavailable to awareness in normal situations. This effect is likely to be induced by a filling-in process, which is triggered by a transient stimulus. The interaction of the filling-in process with veridical spatial representation suggests that, in early cortical areas, the representation of the position of a moving object is still veridical. The perceived position of a moving object should be coded in higher visual areas than those mediating visual filling-in. Recent studies seem to indicate that activity in area MT is critical for the mislocalisation of a moving object (McGraw et al 2004). Also, the representation of an illusory contour is still maintained in early visual areas even when it is not perceived because of motion-induced shift of perceived position (Rajimehr 2004). These lines of evidence suggest that perception of position is not directly encoded in the early areas, but is constructed after combination with motion signals.

References

- Berry M J, Brivanlou I H, Jordan T A, Meister M, 1999 "Anticipation of moving stimuli by the retina" *Nature* **378** 565–566
- Burr D, 1980 "Motion smear" *Nature* **284** 164–165
- De Valois R L, De Valois K K, 1991 "Vernier acuity with stationary moving Gabors" *Vision Research* **31** 1619–1626
- Eagleman D M, Sejnowski T J, 2000 "Motion integration and postdiction in visual awareness" *Science* **287** 2036–2038
- Hazelhoff F, Wiersma H, 1924 "Die Wahrnehmungzeit" *Zeitschrift für Psychologie* **96** 171–188
- Kanai R, Sheth B R, Shimojo S, 2004 "Stopping the motion and sleuthing the flash-lag effect: Spatial uncertainty is the key to positional mislocalization" *Vision Research* **44** 2605–2619
- Khurana B, Watanabe K, Nijhawan R, 2000 "The role of attention in motion extrapolation: Are moving objects 'corrected' or flashed objects attentionally delayed?" *Perception* **29** 675–692
- McGraw P V, Walsh V, Barrett B T, 2004 "Motion-sensitive neurones in V5/MT modulate perceived spatial position" *Current Biology* **14** 1090–1093
- MacKay D M, 1961 "Interactive processes in visual perception", in *Sensory Communication* Ed. W A Rosenblith (Cambridge, MA: MIT Press) pp 339–355
- Macknik S L, Martinez-Conde S, Haglund M M, 2000 "The role of spatiotemporal edges in visibility and visual masking" *Proceedings of the National Academy of Sciences of the USA* **97** 7556–7560
- Mateeff S, Hohnsbein T, 1988 "Perceptual latencies are shorter for motion towards the fovea than for motion away" *Vision Research* **28** 711–719
- Nijhawan R, 1994 "Motion extrapolation in catching" *Nature* **370** 256–257
- Nijhawan R, 2001 "The flash-lag phenomenon: object motion and eye movements" *Perception* **30** 263–282
- Paradiso M A, Nakayama K, 1991 "Brightness perception and filling-in" *Vision Research* **31** 1221–1236
- Rajimehr R, 2004 "Static motion aftereffect does not modulate positional representations in early visual areas" *Brain Research and Cognitive Brain Research* **20** 323–327
- Ramachandran V S, Anstis S M, 1990 "Illusory displacement of equiluminous kinetic edges" *Perception* **19** 611–616
- Sheth B R, Shimojo S, 2003 "Signal strength determines the nature of the relationship between perception and working memory" *Journal of Cognitive Neuroscience* **15** 173–184
- Whitney D, Goltz H C, Thomas C G, Gati J S, Menon R S, Goodale M A, 2003 "Flexible retinotopy: motion-dependent position coding in the visual cortex" *Science* **302** 878–881

ISSN 0301-0066 (print)

ISSN 1468-4233 (electronic)

PERCEPTION

VOLUME 35 2006

www.perceptionweb.com

Conditions of use. This article may be downloaded from the Perception website for personal research by members of subscribing organisations. Authors are entitled to distribute their own article (in printed form or by e-mail) to up to 50 people. This PDF may not be placed on any website (or other online distribution system) without permission of the publisher.